CYCLIC MANIFESTATION OF STERILITY IN BRASSICA PEKINENSIS AND B. CHINENSIS

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(WITH SEVEN FIGURES)

The transition from asexual or vegetative growth to the condition of flower and fruit production in hermaphrodite plants is to be recognized as a most fundamental aspect of sexuality. Furthermore, the inter-relations that exist between vegetative and reproductive vigor and the influence of the former on the latter are reflected and exhibited in certain phenomena of sterility.

It is now certain that vegetative vigor and the internal inter-relations incident to it may limit reproductive vigor and sexuality. The limitation from these causes may take place in two ways: (1) they may interfere with or influence the morphological development of flowers or other reproductive organs, and (2) they may affect the functioning powers of organs that are fully formed. If these influences are marked, one or more types of sterility may appear.

Only recently observations have indicated that, at least in some cases, the compatibilities and the fertility of the sex organs may vary rather definitely within the cycle of vegetative and reproductive development characteristic of the particular species. A phenomenon of this sort is reported by EAST and PARK (4), who found that in the few plants which are self-compatible in certain species and hybrids of *Nicotiana*, the self-compatibility develops only at the end of the flowering period. Cases of cross-compatibility appearing only at the end of the period of bloom are reported also. A very decided case of the development of self-compatibility only at the close of the period of bloom was observed by the writer, in a plant of *Lythrum Salicaria*, and reported at the annual meeting of the Botanical Society of America for 1917. These observations suggested that new evidence on the old problem of the relation between vegetative vigor and reproductive vigor, as expressed in the formation of flowers and the functioning of the

parts in seed formation, may be obtained by experimental means from a study of the fluctuations in fertility that are to be seen in those feebly self-compatible individuals which are to be found in species in which general sexual incompatibilities are strongly developed.

A subsequent report of a more detailed study on this problem (STOUT 11), however, showed that in *Verbascum phoeniceum*, *Eschscholtzia californica*, and *Cichorium Intybus* the various grades of self-compatibility operate very uniformly throughout the entire period of bloom, and that there are in the feebly self-compatible plants of these species no specially marked tendencies to self-compatibility at any definite phase of the blooming period. It was also found that in *Nicotiana Forgetiana* Hyb. Hort. and in *Lythrum Salicaria* end-bloom self-compatibility develops as an infrequent individual variation rather than as a phenomenon characteristic of the self-compatible plants. In these species there is no cyclic production of fruits and seeds which would indicate a general relation between vegetative vigor and the development of self-compatibility.

Such a cyclic occurrence of self-compatibility was found, however, and reported for *Brassica pekinensis*, and it was noted that the highest degree of self-compatibility attained by any given plant appeared very uniformly during the period of mid-bloom. Further studies with this species have since been made which show this to be the rule for all those individuals that are self-compatible in any degree. Similar behavior has also been found in cultures of *Brassica chinensis* and in hybrids between this species and *B. pekinensis*. So far as known to the writer, this is the most uniform and definite case of a general and definite periodicity in the modification of sexual compatibilities within a blooming period. In these species, also, flower abortion appears in the transition of vegetative to reproductive vigor, exhibiting an influence of vegetative vigor on the morphological development of flowers.

Material and methods

Several strains of the "head" sorts of *Brassica pekinensis*, commonly known as Chinese cabbage or Pe-tsai, and one strain of the loose-leaved or headless sort (the Nanking variety) were grown

from seeds furnished by the Office of Foreign Seed and Plant Introduction of the United States Department of Agriculture. The seeds of the strain of *B. chinensis* which have been grown were obtained from China by a Chinese student at Columbia University for the gardener in charge of the greenhouses belonging to the University, and the writer obtained seeds from the first lot of plants there grown. From controlled cross-pollinations between plants of the two species, seeds were obtained and plants of an F_1 hybrid progeny were grown.

The greater number of plants have been grown in pots in a greenhouse and brought into bloom during the winter and spring before they could suffer from the heat of summer. When thus grown, plants of the head varieties of *B. pekinensis* form a rather loose headlike rosette, much smaller and less compact than when grown under field culture, after which they shoot up into flower. Plants of the Nanking variety of *B. pekinensis* and plants of *B. chinensis* do not form a head even under the best of field culture; a very loose rosette of leaves develops, and this grades up into the leaves of the flowering stem. Pot grown plants of these species closely resembled field grown plants except that they were smaller.

A few plants of all strains have been grown to full maturity in the garden, both as spring and autumn crops. Such plants were larger than the pot grown plants and more flowers were produced, but their behavior in respect to fertility and sterility was identical with that of plants grown in the greenhouse. Special effort was taken to make controlled self-pollinations throughout the entire period of blooming.[1] Numerous plants have bloomed alone or in isolation from other species of *Brassica*, both in the greenhouses and in the field, and hand pollinations were made from one to four days apart as long as the plants bloomed. The plants not grown in isolation were "bagged." Flowering branches were inclosed in glassine paper bags on or within a day or two following the opening of the first flowers; the plants were visited at least twice a week (at first

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[1] During the winter season of 1919–1920 the writer was greatly aided by the voluntary assistance of Mrs. MORTIMER J. FOX. Miss HESTER M. RUSK has assisted in the research and made many of the pollinations of the plants grown in 1920–1921. Through this efficient assistance and cooperation the many pollinations necessary to the research were accomplished.

many were visited daily), and pollen from fully dehiscent stamens in liberal amounts was placed on pistils of all freshly opened flowers. After the cyclic modification of self-compatibility was recognized, frequent cross-pollinations were made to test the functional power of pistils and stamens during the periods of self-incompatibility preceding and following the period of mid-bloom. The potency of the pollen has been studied by germination tests, and a cytological study of the phenomena of pollen tube growth and fertilization is under way.

Sterility in Brassica pekinensis and B. chinensis

Three distinct and quite different types of sterility are in evidence during the period of bloom in both these species.

I. One type is to be classed in general with impotence (STOUT 12), but here two very distinct types of impotence may be observed. These may be described as (1) flower abortion of the first flowers, and (2) arrested development of the last flowers that start to form.

II. In some plants of both species, axial proliferations develop from the pistils of many flowers, and the pistils of such flowers are functionless in respect to fruit production.

III. Among the flowers that open fully and are capable of functioning in certain relations, various grades of incompatibilities are in evidence, and self-compatibility whenever present is most strong during the period of mid-bloom.

I. IMPOTENCE

(1) FLOWER ABORTION.—Frequently in *Brassica pekinensis* the first flowers on the main stalk and often also the first flowers on laterals are completely aborted. The flower buds remain small and do not open, but soon become dead and black. A rather characteristic case of flower abortion is shown in fig. 1, which is of a pot grown plant of *B. pekinensis* blooming in February. Nearly forty of the first flowers of the main branch aborted, after which the flowers were completely formed, normal in appearance, and fully capable of functioning in certain fertilizations. The uppermost lateral branch coming into bloom later than the main axis had only five flowers that aborted, and the next lower lateral had no aborted

flowers. On such plants the lateral branches which come into bloom at the time when the main branch is producing normal flowers as a rule have normal flowers from the first (figs. 1–3). This coordination between flowers opening simultaneously on different branches as to kind of development is very marked. At first view, this abortion of flowers appears to resemble the blasting of flowers which frequently occurs in all sorts of plants as the direct effect of unfavorable environmental influences, but here the phenomenon is due primarily to internal conditions. As grown in the various cultures, the plants came into bloom at various times, some were producing mid-bloom and potent flowers, while other plants by them and just coming into bloom showed flower abortion. The abortion, therefore, is essentially self-induced.

Flower abortion of the first flowers is the rule among plants of the varieties of *B. pekinensis* which form leafy heads and which are grown in the field under conditions which favor the development of heads. In such plants, if left to bloom, the flowering branches are at first inclosed within the head. At the time when the flowering branches first come to the light,

FIG. 1.—Typical case of flower abortion in plant of *Brassica pekinensis;* about forty of first flowers on main axis aborted; there are five such flowers on uppermost lateral and none on second lateral, showing correlation in morphological character according to time of blooming.

they are somewhat blanched and tender, and the first flowers are already aborted. This condition of itself suggests that, in this
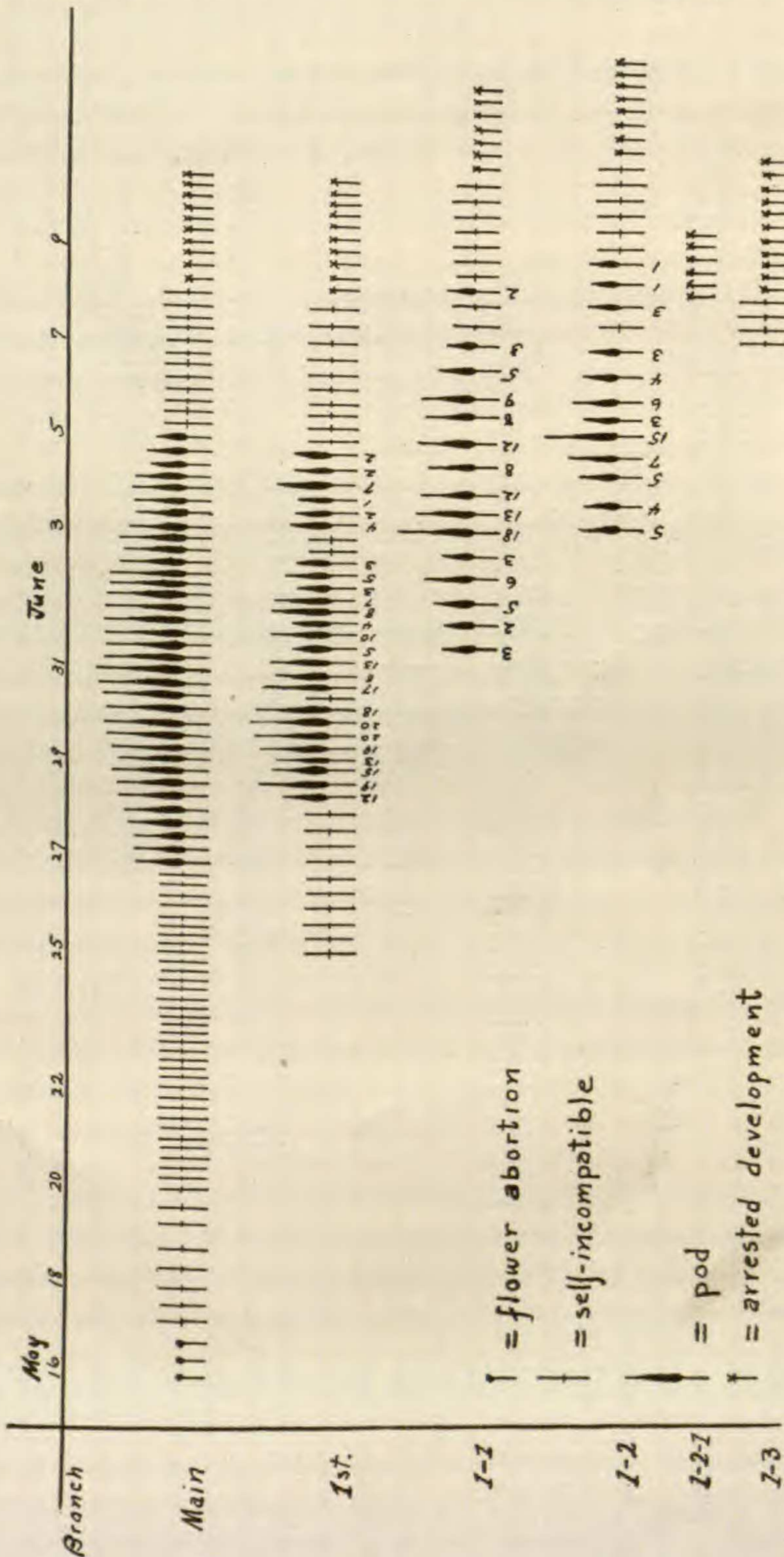

Fig. 2.—Chart showing distribution according to dates of flower abortion, self-incompatibility, self-compatibility, and arrested development on main branch and on uppermost lateral with all its laterals; relative sizes of pods indicated; number of seeds per pod given for all but main branch.

case, temperature and light conditions are important factors which are concerned in the abortion of the first flowers.

Flower abortion, however, is quite pronounced in many plants of *B. pekinensis* grown in pots and in which the head is scarcely
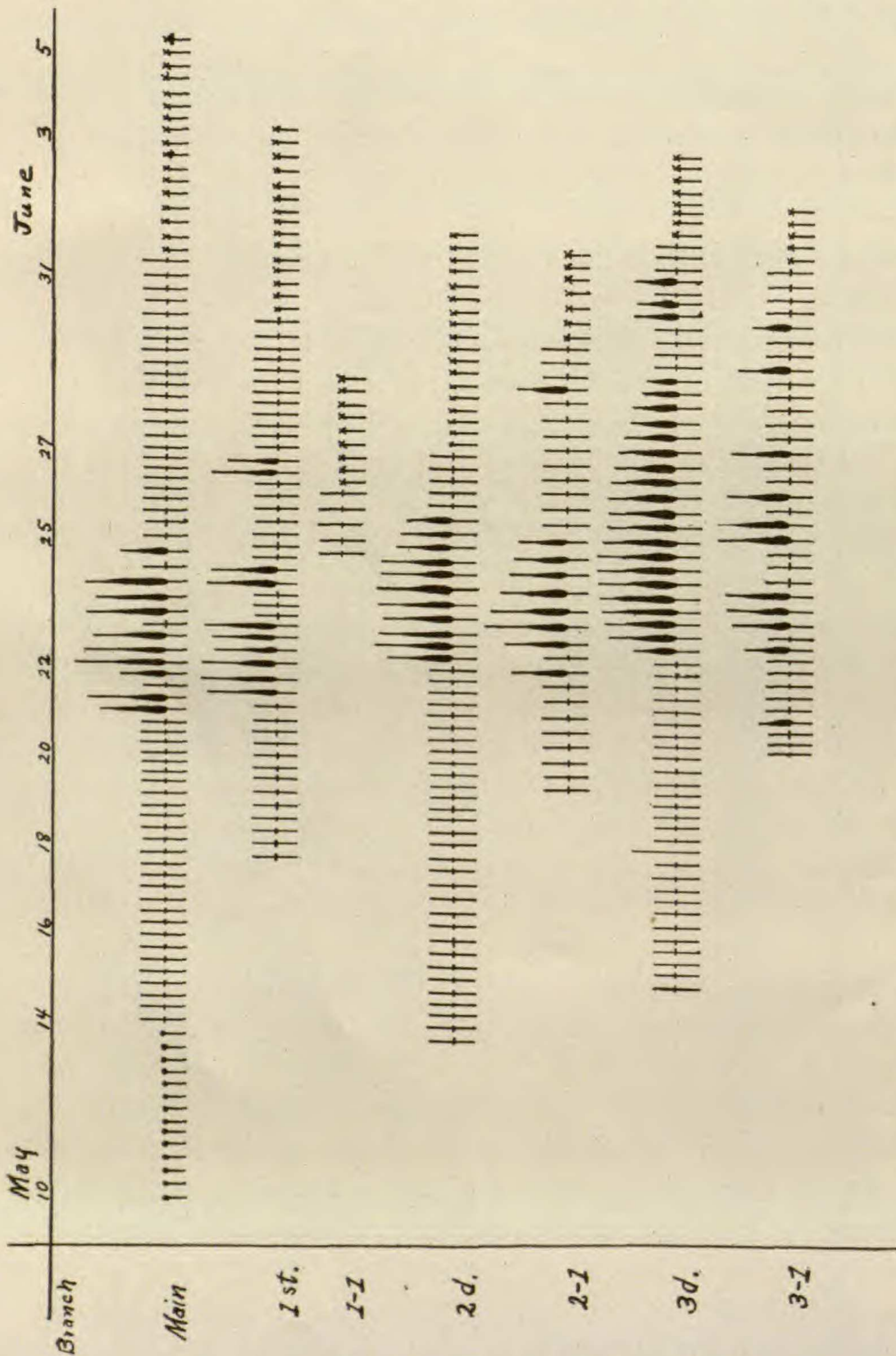

FIG. 3.—Chart for all flowering branches of plant; flower abortion, self-incompatibility, and self-compatibility all cyclic, and each closely coordinated in the various branches according to date of bloom.

developed. In the Nanking variety in which the leaves form only a loose rosette, about one-third of the plants grown have had some

aborted flowers, but usually only a few of the first flowers abort. Flower abortion also appears in many plants of *B. chinensis* which have very loose rosettes of leaves.

In these species flower abortion occurs as a transitional stage between a period of vigorous vegetative vigor and a period of flower formation and seed production. The plants which exhibit abortion are not able to pass at once into complete reproductive activity in producing potent flowers. The amount of abortion is greatest in the varieties of *B. pekinensis* in which vegetative vigor is most marked and in which excessive vegetative growth can readily be induced by good cultural conditions and which have been selected and bred for this feature. Flower abortion occurs in numerous plants of these sorts that are grown in pots, as it does in many plants of the loose-leaved kinds, but it apparently tends to be less marked in these.

Flower abortion is here undoubtedly correlated with the degree of vegetative vigor. It is not merely due to a stifling of flowers from simple direct injury because of inclosure within a head, however, but to a constitutional feature of which the formation of a leafy head or rosette is an extreme expression. In this sense the abortion of flowers is self-induced and to some degree hereditary. Usually the transition from aborted flowers to apparently normal flowers is sudden and complete (fig. 1). Sometimes, however, the first flowers to appear after the aborted ones, or the first flowers when there are no aborted ones, are poorly developed, are plainly immature and undersized, and especially in *B. chinensis* there may be premature opening.

(2) ARRESTED DEVELOPMENT OF LAST FLOWERS.—At least some of the last flowers which begin to form remain immature and functionless. In the first of such flowers the corollas wither quickly and may become dry and papery without falling. Then the flowers become smaller in size and more incomplete in development until at last they are mere stubs of tissue. Usually from six to ten flowers in these various stages of arrested development may be counted at the tip of each branch. On short, lower, lateral branches and on secondary or later laterals all of the flowers may fail to develop fully. This condition is shown in the illustrations. The distribution of flowers that fail to develop is indicated in figs. 2 and 3.

This type of sterility, of course, is very common in all sorts of flowering plants, and is clearly associated with old age and death of the entire plants or of the individual flowering branches. In these species of *Brassica* it is unusually conspicuous, and begins to develop when growth has ceased and parts of the plant, especially the basal leaves, are dying or even dead and falling from the plant. Flowers that have aborted or developed poorly at the beginning of the period of bloom, and those in which development is arrested, are all functionless. Their failure to produce fruit is entirely independent of any sort of fertilization. It is clearly due to impotence.

II. PROLIFERATION

In a few plants of several strains of both *Brassica chinensis* and *B. pekinensis*, noticeable axial proliferations develop. The axis anlage inclosed within the carpels of the pistil grows and branches until it bursts open the pistil. The pedicel of the flower enlarges; the proliferated branch may become several inches long and bear as many as twenty-five flowers, many of which are able to function in seed production. Proliferation may be regarded as the sterilization of a pistil by vegetative growth of the tissue beneath and within it. In the end it is the expression of a tendency to vegetative vigor which culminates in the production of many more pistils and stamens.

Although proliferation is often irregular in its distribution, it is most frequent during the earlier portion of the period of bloom. Frequently it is most highly developed in the first flowers of plants which show little or no flower abortion, but it often does appear later. The last flowers of those which open normally as a rule are free from proliferations. This abnormality is certainly to be regarded as an expression of excess vegetative vigor, as a result of which the axis about which flower parts are grouped resumes active vegetative growth. The stamens in many of the flowers whose axes proliferate seem to be normal, but the pistils are not productive of fruit.

Another type of excessive vegetative vigor is seen in the development of green leaves at the base of each flower, giving a leafy inflorescence. This has only been observed in a few plants, and

its possible relation to the production of flowers and to their impotence has not been determined.

III. Physiological incompatibility

During the phase when the flowers are completely developed, many flowers are produced that are capable of producing pods and seeds. In general the plants produce such flowers in abundance, in succession for a period of about twenty days, and with continuous and rather rapid elongation of branches (cf. fig. 1 with 4 and 6). A free and indiscriminate functioning of the organs in seed production, however, is decidedly limited by incompatibilities in fertilization.

Self-incompatible plants.—Plants may be completely self-incompatible throughout, as was the case for the plant shown in fig. 4. The first six flowers on the main branch aborted, but the very first flowers on the three uppermost laterals were normal. A few flowers at the ends of the branches failed to develop. In all, about seventy flowers on the main branch, forty on each of the first and second laterals, and fifty on the third lateral were capable of functioning. Three lower branches, which bore together about one hundred normal flowers and were like the third lateral in general appearance, were not included in the photograph. This plant grew in isolation in a greenhouse, and self-pollinations were made by hand at least three times a week throughout the period of bloom. At least two hundred flowers were carefully self-pollinated, but not a pod resulted. The pods which were formed on this plant were all from compatible cross-pollinations. Six fine large pods near the base of the main stem were all from flowers that opened rather early; the two first flowers on the first lateral yielded fine pods to a cross; and large pods containing viable seeds were obtained by crossing some of the very last flowers to open normally on the main stem and on the first and second laterals. The stamens were apparently normal throughout the time when flowers opened normally; pollen from many stamens examined at different times was found to be plump and normal in appearance, and the use of pollen in certain crosses covering the entire period of normal bloom resulted in seeds. Such tests have been made repeatedly on

numerous plants with results as noted, which show that the failure to set seed to self-pollination is due to a sexual incompatibility between reproductive elements that are capable of functioning in certain other relations.

A total of 1371 plants of these two species of *Brassica* and hybrids between them have been tested at the time this is

FIG. 4.—Plant of *B. pekinensis*, completely self-incompatible but producing good pods containing viable seeds to compatible crosses at any time while flowers are fully developed.

FIG. 5.—Feebly self-compatible plant of *B. chinensis;* first two flowers and last to open normally on main axis highly fertile in compatible cross.

written, and of these 653 were found to be completely self-incompatible. Plants were thus classed when no pods developed to selfing at any time throughout the entire period of bloom. There were, however, several grades to be seen in respect to the length of time the pistils remained attached to the plant. In the plant shown in fig. 4, with few exceptions, the pistils of flowers

selfed fell soon after the petals had fallen. In other plants, and especially plants of *B. chinensis*, nearly all the pistils of selfed flowers remained attached only during the period of mid-bloom.

Self-compatible plants.—A total of 718 plants of the various cultures grown were self-compatible in some degree. For the
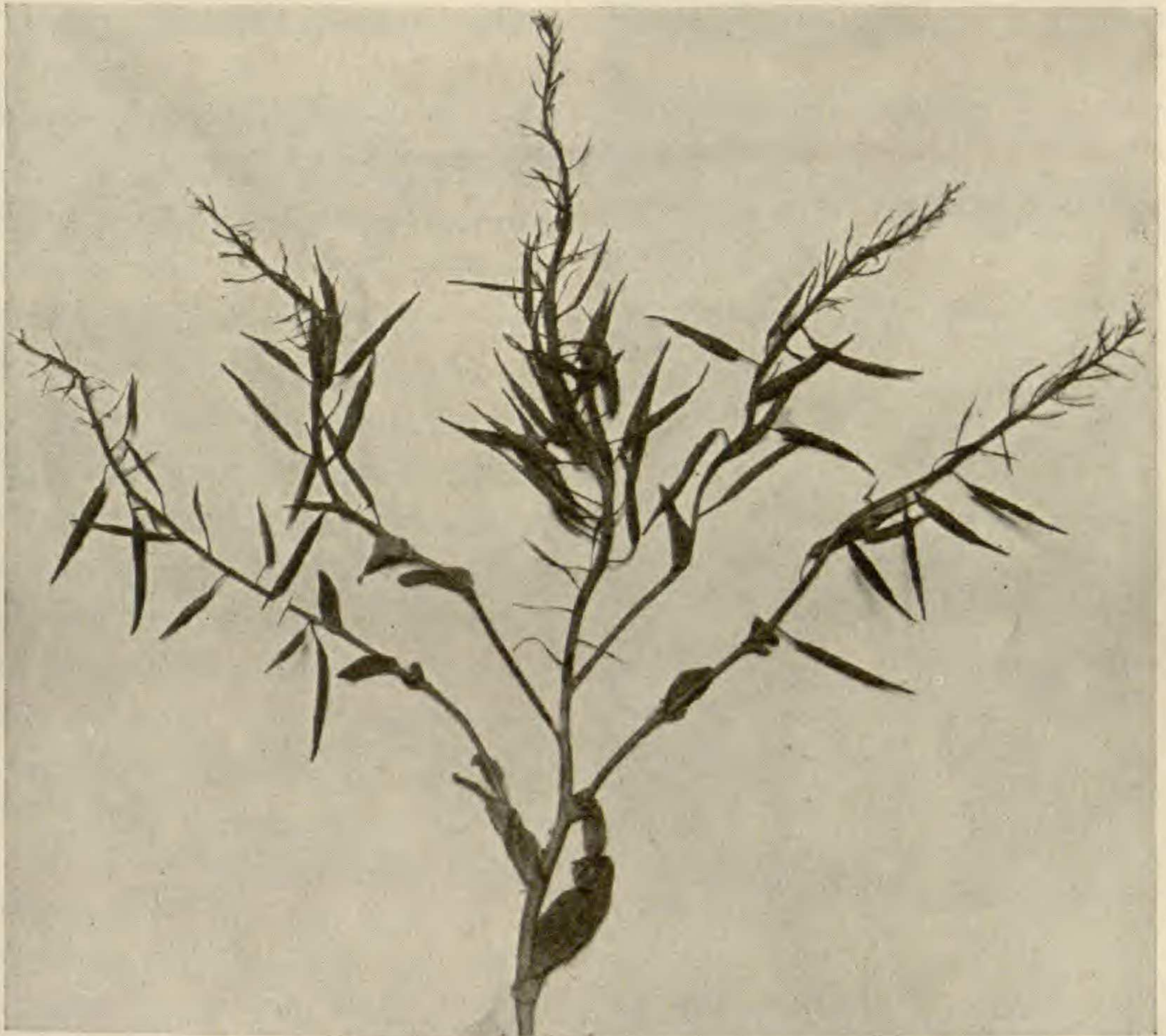

Fig. 6.—Plant of *B. pekinensis*, highly self-compatible during period of mid-bloom; no flower abortion; first flowers to bloom on laterals were self-compatible, showing correlation with main branch in physiological character according to time of bloom.

purpose of a general classification the self-compatibility was judged as *feeble, medium,* and *strong,* but there were many grades within each class with no sharp distinctions between them. The weakest grade includes the cases in which, most typically, a few small pods containing only aborted seeds developed. In some cases pods of good size were formed, as is shown in fig. 5, but the seeds were all

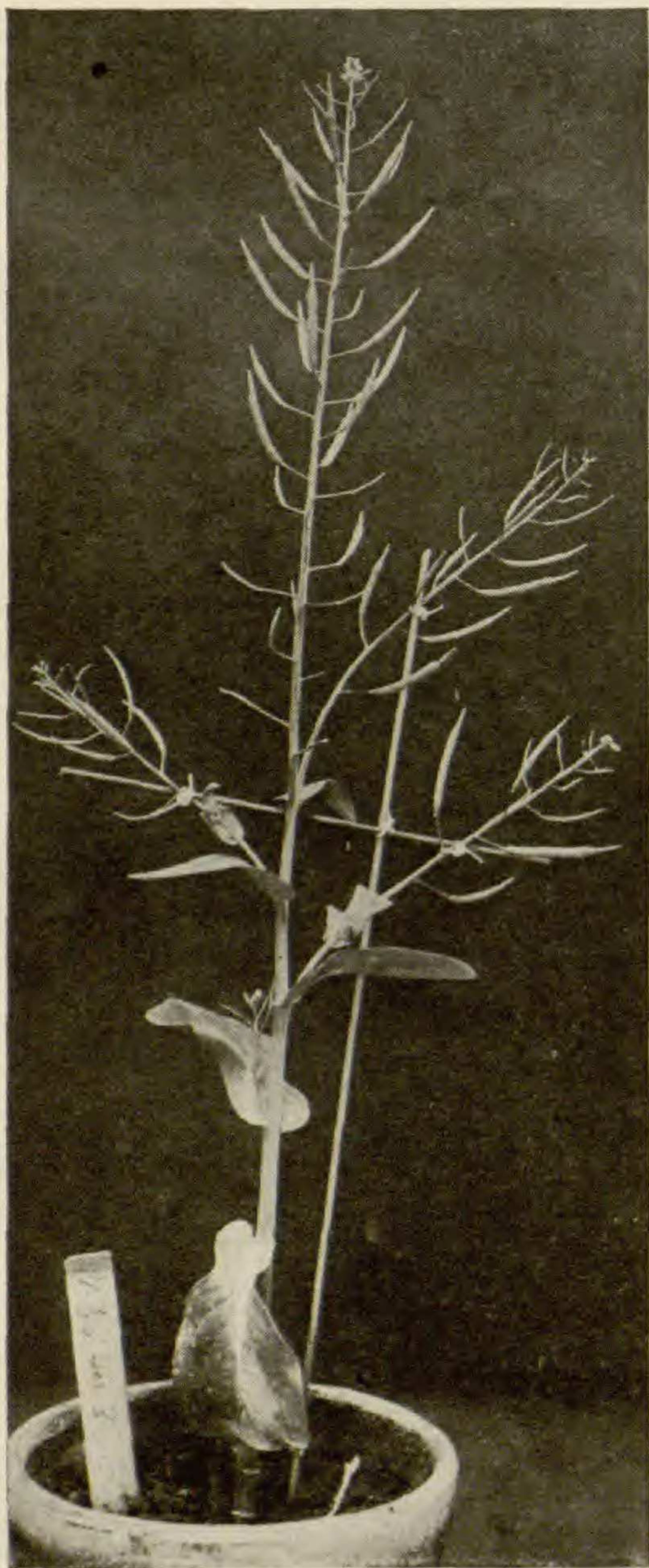shriveled and not viable. Such plants were classed as feebly self-compatible. Plants whose self-compatibility was classed as medium produced some viable seeds. The number of pods, the number of shriveled seeds, and to some extent the number of viable seeds varied greatly among plants thus grouped. The plants classed as strongly self-compatible produced numerous pods, and the total number of viable seeds was high. In these also the number of pods, their size, and the numbers of viable and of shriveled seeds varied greatly. The various grades of self-compatibility were seen among sister plants that were as nearly identical as is possible in regard to vegetative vigor, number of branches and flowers produced, and as to calendar dates for period of blooming.

It was readily recognized that the self-compatibility of such plants was most strong during the period of mid-bloom, and that previous to and following this period there was complete self-incompatibility. A highly self-compatible plant grown in isolation and carefully self-pollinated from day to day appeared at the end of the fruiting period, as shown in figs. 6 and 7. Repeated tests by crossings showed that in these, as in the case of the self-incompatible

Fig. 7.—Plant of *B. chinensis;* no flower abortion; plant highly self-compatible; showing cycle of self-compatibility with climax at time of mid-bloom.

plants, the flowers that opened normally during the time of self-incompatibility were functional in compatible crosses. The results of a test of this sort are shown in fig. 5. The cyclic development of self-compatibility with its coordination among the various branches of an individual according to time of bloom is shown in figs. 2 and 3.

There is evidence from other species (SIRKS 10) that various grades of cross-compatibility may exist between the individuals of the same race or species, that the group relations may be variable in different cultures of the same species or race (EAST and PARK 4), and that in general cross-incompatibilities appear with much the same irregularity in heredity and in expression as do self-incompatibilities.

The writer's studies with these plants have been chiefly concerned with self-compatibility. In the species of *Brassica* studied the cross-relations have not been studied sufficiently to state with certainty whether the grades of cross-incompatibility undergo cyclic changes like those of self-incompatibility, but perhaps it may be assumed that certain of the weaker grades of cross-incompatibility do thus operate.

Heredity of mid-bloom self-compatibility in pedigreed lines of descent

In the first or "parent" series grown of both *Brassica pekinensis* and *B. chinensis*, of a total of 253 plants there were 21 plants that produced viable seeds to self-pollination during the period of mid-bloom. From such seeds pedigreed progenies were grown through two generations, to test the inheritance of self-compatibility and to determine the result of repeated selection for this character. A summary of the records for the various series and families grown to date is presented in table I. In these records the first series of plants grown are given arbitrary numbers. The number of a series with that of the self-compatible plant used as a seed parent is employed in designating the series of succeeding generations. Thus the line of descent and the relationship of the various series of sister plants are fully indicated.

In one series of the selfed F_1 generation of *B. pekinensis* (series 1-2) comprising 88 plants, 24 were strongly self-compatible. In

TABLE I

RECORDS OF SELF-COMPATIBILITY FOR FAMILIES OF *Brassica pekinensis*, OF *B. chinensis*, AND OF HYBRIDS BETWEEN THESE SPECIES

| | | | RECORD FOR PROGENY | | |
| | | | Self-compatible | | |
ANCESTRY, GENERATION, AND SELF-COMPATIBILITY OF PARENT	Total number of plants	Number self-incompatible	Feeble	Medium	Strong
Brassica pekinensis					
P series 1, seeds of S.P.I. no. 44892	9	7	0	1	1
P series 2, seeds of S.P.I. no. 44935	10	6	2	1	1
P series 3, seeds of S.P.I. no. 44291	20	19	0	1	0
P series 4, seeds of S.P.I. no. 44312	12	9	1	0	2
P series 5, seeds of S.P.I. no. 44292	8	8	0	0	0
P series 34, seeds of S.P.I. no. 38783	114	67	45	2	0
P series 15, seeds of S.P.I. no. 45187	61	55	5	1	0
F_1 series 1–2, parent strongly self-compatible	88	25	19	20	24
F_1 series 2–1, parent strongly self-compatible	7	7	0	0	0
F_1 series 3–1, parent medium self-compatible	80	43	27	7	3
F_2 series 1–2–9, parent strongly self-compatible	36	5	19	9	3
F_2 series 1–2–18, parent strongly self-compatible	133	14	99	18	2
F_2 series 1–2–29, parent strongly self-compatible	46	24	21	1	0
F_2 series 1–2–38, parent strongly self-compatible	60	1	43	15	1
F_2 series 3–1–1, parent strongly self-compatible	19	15	2	2	0
F_2 series 3–1–9, parent strongly self-compatible	16	10	6	0	0
F_2 series 3–1–32, parent strongly self-compatible	18	12	6	0	0
Brassica chinensis					
P series 8..	19	4	4	8	3
F_1 series 8–1, parent strongly self-compatible	111	42	56	12	1
F_1 series 8–5, parent medium self-compatible	48	43	3	2	0
F_1 series 8–6, parent strongly self-compatible	57	28	26	2	1
F_1 series 8–15, parent strongly self-compatible	122	40	74	7	1
F_2 series 8–1–13, parent strongly self-compatible	13	7	5	1	0
F_2 series 8–5–32, parent medium self-compatible	18	7	10	1	0
F_2 series 8–5–39, parent medium self-compatible	9	7	1	1	0
F_2 series 8–15–5, parent strongly self-compatible	48	30	16	2	0
F_2 series 8–1, no. 39×8–1 no. 32 (medium×medium)	30	23	7	0	0
F_2 series 8–5, no. 39×8–5 no. 41 (medium×self-sterile) ...	32	15	17	0	0
F_2 series 8–5, no. 30×8–5 no. 17 (both self-sterile) ....:	16	15	1	0	0
F_2 series 8–5, no. 27×8–5 no. 32 (self-sterile×medium) ...	8	7	0	1	0
Brassica chinensis×B. pekinensis					
F_1 8–5, no. 23×2 no. 3 (both self-incompatible)	19	19	0	0	0
F_1 8–5, no. 19×3 no. 16 (both self-incompatible)	34	27	5	2	0
F_1 8–5, no. 18×3–1 no. 63 (medium×self-sterile)	50	12	14	19	5

the next generation of this family, the progeny of four strongly self-compatible plants, 275 plants were grown. Of these only 44 were completely self-incompatible. There were, however, only 6 plants as highly self-compatible as the immediate seed parents. The majority of the plants (182 in number) were feebly self-compatible and did not produce any viable seeds to selfing. This family, however, was somewhat more highly self-compatible than was the family derived from plant no. 1 of series 3, in the second generation of which only 2 plants out of 53 produced viable seeds to selfing.

Selection for the highest grades of self-compatibility in *B. chinensis* was also carried through the second generation. In the F_1 generation, 26 out of 338 plants produced viable seeds to selfing. In the F_2, 5 out of 88 plants produced such seeds. The proportion of self-compatible plants was low and remained about the same, not being appreciably increased or decreased in the second generation. No plants classed as highly self-compatible were found in the F_2, but this may have been due to the proportionally smaller number of plants grown in this generation.

Four series comprising 86 plants were grown from seeds obtained by crossing certain plants of the F_1. Of these, 25 were feebly self-compatible and one plant produced viable seeds. The F_1 hybrids between the two species exhibited the three types of sterility characteristic of the parent species. There was no indication of a general impotence of both sex organs (pistils and stamens) such as often results from hybridity. During the time when flowers opened normally, branches left to open pollination produced pods and viable seeds, and about 100 plants of this generation grown in the field and left to open cross-pollination produced pods in abundance.

As to mid-bloom self-compatibility, the F_1 hybrids were like the pure bred parents. Relatively few were highly self-compatible. In one series, derived from crossing a plant of a medium grade self-compatibility and one completely self-incompatible, of 50 plants, 12 were fully self-incompatible, 14 were feebly self-compatible, 19 were self-compatible of medium grade, and 5 were

highly self-compatible. Two series were grown from parents that were self-incompatible. In one of these all of the 19 progeny were self-incompatible; in the other series of 34 plants 27 were fully self-incompatible, 5 were feebly self-compatible, and 2 were self-compatible of medium grade during the period of mid-bloom.

SUMMARY.—The results obtained in these various pedigreed cultures show that self-compatibility is a character which is not directly hereditary. Self-compatibility occurs sporadically in a few members of these prevailing self-incompatible species. This character does not breed true. Selection for self-compatibility does not immediately lead to the establishment of self-compatible races. Neither is self-compatibility nor self-incompatibility dominant in crosses. There is some indication, however, that certain races may be secured in which the mode of distribution in respect to self-compatibility is higher than in others.

Discussion and conclusion

The strains of *Brassica pekinensis* and *B. chinensis* studied were previously selected and bred for excessive leafy growth rather than for fruit and seed production, yet they are reproduced exclusively by seeds. The vegetative vigor is not in the least utilized in the development of parts which may propagate the plants vegetatively. In their habit of growth and bloom, the stage of sexual reproduction in these plants quickly follows a period of remarkably vigorous vegetative development, hence these species are favorable material in which to study the correlative relations of the asexual or the vegetative phase to the sexual or reproductive (by seeds) phase in the complete life cycle.

The two types of sterility, impotence (including flower abortion and arrested development), and proliferation, or the destruction of a pistil by vegetative growth, as they occur in *B. pekinensis* and *B. chinensis*, are both phenomena associated with the formation of floral organs. The other type of sterility, physiological incompatibility or relative sterility which is present, is concerned with the physiological inter-relations of the sex organs in the various processes of fertilization.

These three types of sterility develop and operate in these two species and in their hybrids in intimate correlation with the cyclic

alternation of vegetative and reproductive vigor. Flower abortion occurs normally as a transitional stage between the formation of green leaves and the production of functional sporophylls. Those plants which exhibit flower abortion are not able to pass directly from producing green leaves or leaves with branches at the nodes to the production of flowers, and flower abortion occurs as a transitional stage. The abortion of flowers appears in the phase where vegetative vigor is waning, but before reproductive vigor is fully in evidence. There is also a marked agreement among the various branches of a plant as to the grade of development reached at any one date of blooming (figs. 1–3), which indicates a definite relation between the condition causing flower abortion (and also normal flower formation) and a condition of the plant as a whole. These phenomena, therefore, have many aspects characteristic of physiological correlation.

The arrested development of flowers at the ends of branches after a period of vigorous blooming of the plant is obviously due to an extreme waning of vigor and the approaching death of the plant as a whole, and of course is a phenomenon prevalent in all sorts of plants. Axial proliferation from the pistils is to be considered as a resumption of vegetative growth after the differentiation of the pistils has been accomplished.

Turning to the functional relations of the sex organs in these two species of *Brassica*, at least to the compatibility in self-fertilization, it is seen that they also exhibit a periodicity on their occurrence which forms a very definite cycle. A total of 718 plants that were self-compatible to some degree have now been observed in these two species and in hybrids between them. With the exception of a few individuals in which pods developed irregularly, the maximum of self-compatibility was reached during the mid-bloom of the plant (figs. 2, 3, 5–7). Previous to and following this period, the self-compatibility grades into complete self-incompatibility or into a much weaker grade of self-compatibility. Furthermore, the climax of self-compatibility is remarkably coordinated among the different branches according to the time of blooming quite as is the earlier development of flower abortion.

The remarkably uniform development of self-compatibility during the time of mid-bloom in *Brassica chinensis*, *B. pekinensis*,

and hybrids between them, is convincing evidence that the functions of fertilization are here operating in a cycle of intensities. The period of mid-bloom may be considered as the time when conditions are most favorable for fertilization. The cross-fertilizations which are highly effective both previous to and following the maximum for self-compatibility are hence to be considered as indicating a different and possibly a stronger grade of sexual relation. It seems conclusive that, judged by the functional relations in fertilization, the physiological properties of the sex organs in these plants vary in a rather definite cycle.

It is clear that self-compatibility as contrasted with certain grades of cross-compatibility in these species of *Brassica* is limited to a specific period following the transition from vegetative to reproductive activity and limited by the waning senility of the plant as a whole. Self-compatibility appears coincidently with the climax of the reproductive activity.

Sexual reproduction itself is generally characterized as a phenomenon of maturity (COULTER 3). The differentiations of sex as indicated by anatomical features and by the physiological compatibilities are perhaps to be considered as a smaller cycle operating within the larger alternation of vegetative and reproductive phases and subject to the same biogenetic regulation.

In the flowering plants especially, there is great diversity among species in the relative development of their vegetative and reproductive habits and in the inter-relations between these two phases. Perhaps the most universal of the biogenetic conditions incident to the transition from the vegetative to the reproductive phase is that change in nutrition which leads to the accumulation of carbon compounds. This is an internal condition that arises in the plant as a whole in the course of maturity, in contrast with relative excess of nitrogenous material that is characteristic of the vegetative stage. The decided influence of nutritive relations in regulating development and in influencing fruitfulness has recently been discussed by KRAUS and KRAYBILL (7), who have emphasized the fact that a well-balanced development, especially in regard to fruitfulness of fruit-bearing plants, is associated with a proper balance between nitrogen and carbohydrate metabolism.

It is not to be considered, however, that a single simple change in nutrition is the sole biogenetic factor regulating the appearance of maturity and its attending morphogenesis of flowers. In flowering plants, such as the species of *Brassica* whose sterilities are reported in this paper, there is progressive differentiation of parts in reference to metabolic activities which is most obvious in respect to the manufacture, distribution, and consumption of food. It has been shown that there are also special stimulating and inhibiting influences which in a decided manner regulate and correlate development. That these influences may be substantive and special (but metabolic) and different from food materials was postulated by SACHS (8) in one of the latest of his papers; that some influences are stimulative and correlative in the sense of nervelike impulses or even electrical stimuli have repeatedly been shown in studies of the nature of transmission and excitation in phenomena of dominance and control in correlative growth and development (CHILD 1).

It is to be noted that the complete life cycle of flowering plants involves two periods of vegetative vigor and maturity; one for the sporophyte and one for the gametophyte. The former culminates in the production of spores and the latter in the production of gametes. The generations are antithetic. In its length of life, vigor of vegetative growth, and reproductive power (number of gametes), the gametophytic phase has become relatively weak and highly specialized. In the sporophyte great vegetative vigor is correlated with great reproductive vigor in the production of spores (which are, however, in themselves asexual) and in the nurture of the gametophyte and the embryo. Sex differentiation in the great group of flowering plants has been pushed back during the progress of evolution into the sporophytic stage of the entire cycle, and here sexuality now culminates in seed formation in which the nutrition of the embryo is a most important factor. Sexual reproduction in these higher plants has become more and more inter-related with the vegetative phase of the sporophyte and subject to its internal and biogenetic regulation.

The decided influence of such regulation is seen in the fact that in the great group of hermaphrodite plants, the whole trend of the

morphological and physiological differentiations constituting sexuality is initiated in the morphogenesis of flowers. The cells of pistils and stamens are not only alike in their preformed genetic composition, but they are identical in this particular with the cells that entered into the preceding vegetative structures. CORRENS (2) has noted that the regeneration from sister cells of the egg and sperm (the archegonial and antheridial cells) in certain monoecious mosses shows that, at least in hermaphrodites and monoecious plants, maleness and femaleness are carried equally by both male and female gametes. The male gametophytes and their most highly specialized male cells are male only because of a temporary suppression of femaleness. Likewise the femaleness of egg cells is a temporary and one-sided expression of cells carrying both sex potencies. The various expressions of maleness and femaleness even in the sex generation, at least in hermaphrodite plants, according to CORRENS, are "phenotypic" or biogenetic expressions independent of any qualitative differentiation in the component units of the germ plasm. The expressions of the so-called factors for sex or the so-called inhibitors of one or the other sex are hence independent of corresponding differentiations in germ plasm which may have arisen during sporogenesis. The expression of sex, therefore, is on the same basis as are the somatic differentiations that arise among the various parts of the individual. It hence becomes a most fundamental biological problem to consider and to determine as far as possible what conditions determine these differences in the level of the so-called "physiological gradient."

Maturity, with its transition from the vegetative to the reproductive phase, whether giving homologous or antithetic alternation or a continuation of either, occurs in cycle after cycle with remarkable uniformity. This emphasizes the phylogenetic or hereditary aspect of particular phases of the development. One may assume a "gene" or a "factor" for maturity, and assume that it is gradually awakened from a dormant condition to the exercise of its influence at a particular time and in a particular group of cells. One may further assume that the loss of such a gene would throw a line of progeny into a condition of perpetual immaturity, so that flowers or other reproductive organs could never be formed. The evidence

is decidedly against such a view. The loss of maturity, as seen especially in the complete failure of flower formation, has very universally been shown to be due to the indirect influence of such external factors as light, heat, and nutrition on the metabolism and attending correlations in the organism (see numerous papers by MÖBIUS, VÖCHTING, KLEBS, SACHS, and GOEBEL, and recent papers by GARNER and ALLARD 5 and 6, and by SETCHELL 9).

That species or strains showing flower abortion and physiological incompatibility are different genetically from others that do not show such sterilities is obvious. That these types of sterility are more completely hereditary in some species than in others is clear. That these characteristics are not definitely and directly represented as such in the germ plasm by hereditary units is very evident from the results of genetical studies. Self-compatibility and self-incompatibility especially are not found to be alternative conditions in tests by crossing or in line breeding; the heredity is decidedly irregular and sporadic even when compatibilities are not cyclic in their appearance as they are in *Brassica chinensis* and *B. pekinensis*.

The various types of sterility seen in these species of *Brassica* decidedly indicate a mutually limiting relationship between vegetative and reproductive vigor. Their irregular inheritance, their appearance at definite periods in the cycle of development of the plant as a whole, and especially the cyclic manifestation of self-compatibility, indicate that the morphological and physiological differentiations of sex are regulated and determined by those internal and biogenetic processes which in general determine the cycle of growth, development, and maturity in the life of the individual.

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